

S-111-1

MUS. COMP. ZOOL.
LIBRARY

JUN 21 1966

HARVARD
UNIVERSITY

TRANSACTIONS
OF THE
SAN DIEGO SOCIETY OF NATURAL HISTORY

VOLUME 14, No. 11, pp. 137-156

BIOGEOGRAPHY AND DISTRIBUTION OF
THE REPTILES AND AMPHIBIANS ON ISLANDS
IN THE GULF OF CALIFORNIA, MEXICO

BY

MICHAEL SOULÉ

Stanford University, Stanford, California
(Present address: University of Malawi, Limbe, Malawi)

AND

ALLAN J. SLOAN

Assistant Curator of Reptiles and Amphibians
San Diego Natural History Museum

SAN DIEGO, CALIFORNIA

PRINTED FOR THE SOCIETY

JUNE 10, 1966

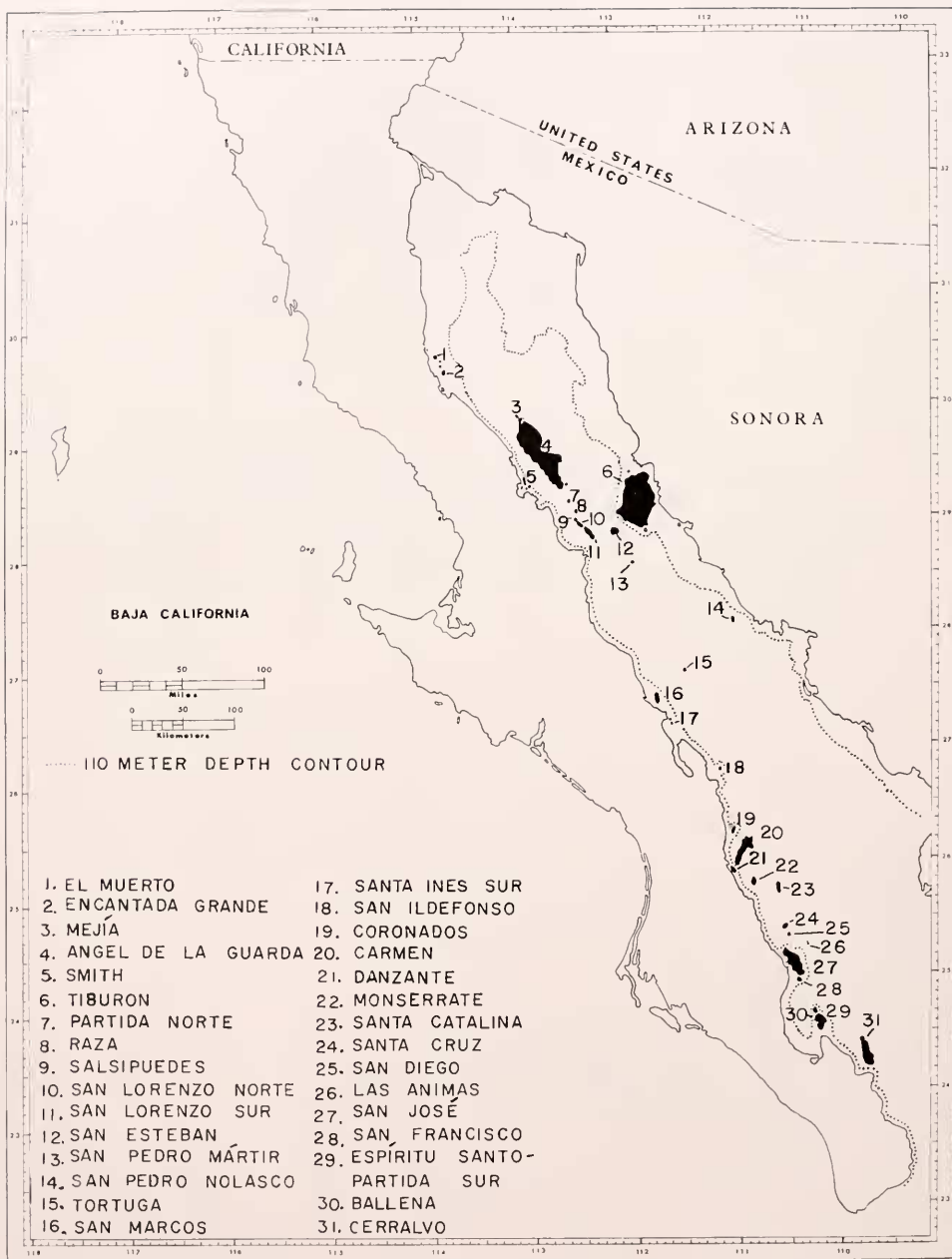


Fig. 1. Islands in the Gulf of California referred to in this report.

JUN 21 1966

HARVARD
UNIVERSITY

BIOGEOGRAPHY AND DISTRIBUTION OF THE REPTILES AND AMPHIBIANS ON ISLANDS IN THE GULF OF CALIFORNIA, MEXICO

BY

MICHAEL SOULÉ AND ALLAN J. SLOAN

INTRODUCTION

The first comprehensive analysis of the herpetofauna of the islands in the Gulf of California was that by Schmidt (1922); in his report of the results of the 1911 "Albatross" expedition, 54 records of island reptiles are given. In 1921 most of the islands were visited by the California Academy of Sciences' "Silvergate" expedition under the leadership of Joseph Slevin. Van Denburgh's (1922) tabulation of 127 records from the Gulf islands includes the material collected by the "Silvergate" personnel. Cliff (1954a) studied the Gulf island herpetofauna and published on the snakes (1954b). At that time the total known reptile fauna amounted to some 200 insular populations. Since then about 50 new records have accumulated. Responsible for the acquisition of much of this new material was the Belvedere expedition to the Gulf in the spring of 1962. Lindsay (1962) provided an account of the Belvedere expedition in which he mentioned many of the new records which are formally presented here.

Many persons and institutions have made important contributions to this project. Charles E. Shaw, of the Zoological Society of San Diego, and the senior author were responsible for the collection of reptiles obtained on the Belvedere expedition, although all the biologists contributed. Permits to collect reptiles in the Republic of Mexico were granted by the late Luis Macias Arellano, and Rodolfo Hernandez Corzo, Dirección General de Caza, Departamento de Conservación de la Fauna Silvestre. Field work has been supported by grants from the Belvedere Scientific Fund and the National Science Foundation (G-14426, GB-2317), and donations from Richard M. Adcock, Richard F. Dwyer, and Roy E. Marquardt.

Basis for Taxonomic Decisions.—Many of the Gulf populations are known by two or more names. The majority of these taxonomic uncertainties stem from differences of opinion as to whether a population deserves specific or subspecific recognition. Where decisions as to specific or subspecific rank of insular populations have been necessary, we have in general followed the suggestion of Mayr (1942:121): "If we examine the 'good' species of a certain locality we find that the reproductive gap is associated with a certain degree of morphological difference. If we find a new group of individuals at a different locality, we use the scale of differences between the species of the familiar area to help us in determining whether the new form is a different species or not. These scales of differences are empirically reached and differ in every family and genus."

Comments on Distribution Table.—The distribution of reptiles and amphibians on islands in the Gulf of California is shown in table 1. The table includes 15 new records reported in this paper (see below). The islands are arranged approximately from north (left side of table) to south. Several very small islands close to the mainland on either side of the Gulf, as those in Bahías de los Angeles, Concepción, and Kino, and near Mazatlán, are not listed. Several very small satellite islands from which only one or two lizards are known are also omitted. References for the table are: Banks and Farmer, 1963; Banta and Leviton, 1963; Cliff, 1954a, 1954b, 1958; Crippen, 1962; Dickerson, 1919; Dixon, 1964; Etheridge, 1961; Figg-Hoblyn and Banta, 1957; Klauber, 1956, 1963; Lowe and Norris, 1955; Savage and Cliff, 1954; Schmidt, 1922; Shaw, 1945; Smith and Taylor, 1945, 1950; Soulé, 1961 and in preparation; Van Denburgh, 1922; Zweifel and Norris, 1955. The location of the islands is shown in figure 1.

New Records of Snakes

This section contains data on a number of snakes which appear to represent new Gulf island records. Except as noted, the specimens referred to are in the collection of the San Diego Society of Natural History (SDSNH).

TABLE 1 (Continued)

Species of native land mammals ¹	Area in square kilometers	Maximum altitude in meters
<i>Cnemidophorus tigris celeripes</i>	1	192
<i>Cnemidophorus tigris dickersonae</i> ⁵	3	1316
<i>Cnemidophorus tigris estebanensis</i>	2	262
<i>Cnemidophorus tigris gracilis</i>	7	223
<i>Cnemidophorus tigris martyni</i>	Encantada Grande	0.9
<i>Cnemidophorus tigris rubidus</i>	Mejia	3.5
<i>Leptotyphlops humilis slevini</i>	Angel de la Guardia	4.5
<i>Lichanura trivirgata gracia</i>	Smith	1
<i>Lichanura trivirgata trivirgata</i>		
<i>Chilomeniscus cinctus</i>		
<i>Chilomeniscus punctatissimus</i> ⁴		
<i>Chilomeniscus savagei</i>		
<i>Eridiphas slevini</i>		
<i>Hypsiglena ochrorhyncha</i> ssp.		
<i>Hypsiglena ochrorhyncha gularis</i>		
<i>Hypsiglena ochrorhyncha ochrorhyncha</i>		
<i>Hypsiglena ochrorhyncha tortrigaensis</i>		
<i>Hypsiglena ochrorhyncha venusta</i>		
<i>Lampropeltis getulius californiae</i>		
<i>Lampropeltis getulius catalinensis</i>		
	El Muerto	0.9
	Encantada Grande	7
	Mejia	3.5
	Angel de la Guardia	4.5
	Smith	1
	Tiburón	1218
	Parida Norte	2.1
	Raza	1.1
	Salsipuedes	1.8
	San Lorenzo Norte	8.5
	San Lorenzo Sur	44.5
	San Esteban	43
	San Pedro Mátrix	1.8
	San Pedro Nolasco	3.2
	Toruga	6.3
	San Marcos	31.5
	Santa Inés (Sur)	< .5
	San Ildefonso	2.6
	Coronados	8.5
	Carmen	151
	Danzante	4.9
	Monserate	19.4
	Santa Catalina	43
	Santa Cruz	11.6
	San Diego	1.3
	Las Animas	< .5
	San José	194
	San Francisco	2.6
	Espiritu Santo-Parida	99
	Balleña	< .5
	Cerralvo	163

<i>Masticophis bilineatus bilineatus</i>	C	R	C C C C	C C C C	C C C
<i>Masticophis bilineatus slevini</i>	C				
<i>Masticophis flagellum piceus</i>					
<i>Masticophis lateralis barbouri</i>					
<i>Phyllorhynchus decurtatus arenicola</i>				R	C
<i>Phyllorhynchus decurtatus decurtatus</i>					
<i>Phyllorhynchus decurtatus perkinsi</i>	C				
<i>Pituophis melanoleucus affinis</i>	C				C
<i>Rhinocheilus lecontei lecontei</i>	C				
<i>Salvadora hexalepis hexalepis</i>					
<i>Salvadora hexalepis klauberi</i>					C
<i>Sonora mosaueri</i>					C
<i>Tamilla planiceps</i>			C		
<i>Trimorphodon lyrophanes</i>					
<i>Microroides euryxanthus euryxanthus</i>	C				C
<i>Crotalus atrox</i> ¹⁰	C	C			
<i>Crotalus catalinensis</i>				S	
<i>Crotalus cerastes cercobombus</i>	C				
<i>Crotalus enyo cerrahensis</i>					R
<i>Crotalus enyo enyo</i>			C		C C C
<i>Crotalus mitchelli angelensis</i>					
<i>Crotalus mitchelli mitchelli</i>				C	C C C
<i>Crotalus mitchelli muertensis</i>					
<i>Crotalus mitchelli pyrrhus</i>	R				
<i>Crotalus molossus estebanensis</i>	C				
<i>Crotalus molossus molossus</i>	C				
<i>Crotalus ruber lucasensis</i>					C
<i>Crotalus ruber ruber</i> ⁵	C			C	
<i>Crotalus tortugensis</i>				S	
<i>Gopherus agassizi</i>	C				C C
<i>Bufo punctatus</i>	C				C
<i>Scaphiopus coxchi</i>					

¹Excluding bats; information courtesy of Richard C. Banks. ²Also occurs on Gallina. ³Also occurs on Pond, Pelicano, Cayo, and Coyote. ⁴Questionable status. ⁵Also occurs on Pond. ⁶Also occurs on Lobos. ⁷Also occurs on Granite and Pond. ⁸Also occurs on Lobos (sight record), and Pelicano. ⁹Also occurs on Chuludo, Colorado, Granite, Patos, Pelicano, Las Galeras, and Coyote. Lower case letters indicate similar populations (Soulé, in prep.). ¹⁰Also occurs on Turners.

Leptotyphlops humilis slevini Klauber. The single blind snake collected during the Belevedere expedition constitutes an addition to the herpetofauna of Isla Carmen. A female (SDSNH 44386) was found near Bahía Marquer by Charles E. Shaw and George E. Lindsay, April 4, 1962. The total length is 221 mm., the tail length, 8 mm. There are 14 scale rows at midbody, 14 subcaudals, 240 scales between the rostral and tail spine, and 12 scale rows around the tail. The first four median dorsal scales are nearly equal in size. The seven dorsal scale rows are medium brown.

This specimen is assigned to the subspecies *slevini* until additional specimens are available to determine the variation in this island population. Most characters are within the range of variation ascribed to this subspecies by Klauber (1940a:133). The number of dorsal scales is lower, and is very close to the mean number for *dugesii*. This specimen is darker than typical *slevini*, although not nearly as dark as coastal *humilis*.

The only previous report of worm snakes on Gulf islands is that by Banks and Farmer (1963) for Isla Cerralvo.

Lichanura trivirgata gracia Klauber. An adult female (SDSNH 51999) was collected by Howard E. Everette at Puerto Refugio, on the north end of Isla Angel de la Guarda, March 19, 1963. It was found about two hours after sundown.

This specimen has a total length of 724 mm., and a tail length of 90 mm. There are 235 ventrals, 49 subcaudals, and 41 scale rows at midbody. The three longitudinal stripes are orange-brown, and adhere closely to the edges of the limiting scales. Unlike typical specimens of this subspecies, which have drab ground color, the dorsal ground color is light to medium gray, and the stripes tend to be outlined in black. This black outline is particularly prominent on the lower edge of each lateral stripe, and is composed of a concentration of minute black spots on the inner edges of adjacent scales. This specimen is similar in coloration to one from six miles south of Socorro, in northern Baja California (considered a possible intergrade by Klauber, 1931a:312), and to recently collected material from the peninsula opposite the island.

The ovary of this snake contains eggs of three distinct size classes. Five eggs average 6.8×7.2 mm., six average 2.5×3.2 mm., and eight others are less than 1 mm. in greatest diameter.

The desert rosy boa was expected to occur on Isla Angel de la Guarda since a dried example was collected on nearby Isla Mejía by Joseph R. Slevin in 1921 (Van Denburgh, 1922:633).

Lichanura trivirgata trivirgata Cope. Two specimens of this subspecies were collected during the Belvedere expedition, and represent the first insular records of this subspecies.

An adult male (SDSNH 52898) was secured in Arroyo Sausal, on the southwest side of Isla Tiburon, March 20, 1962, by Charles F. Harbison. This snake is 678 mm. long, including the 84 mm. tail. There are 222 ventrals, 45 subcaudals, and 37 scale rows at midbody. The second specimen is also an adult male (SDSNH 44389), collected in Arroyo de los Chivos, on the northwest side of Isla San Marcos, March 29, 1962, by Richard C. Banks. The total length is 627 mm., the tail length, 79 mm. There are 217 ventrals, 41 subcaudals, and 39 scale rows at midbody.

Both specimens have the typical coloration and contrasting pattern (dark brown stripes on a cream colored background) of southern Baja California material; however, the San Marcos snake has exceptionally wide stripes.

Lampropeltis getulus californiae (Blainville). The California king snake is tentatively added to the faunas of three islands in the Gulf of California, Islas Angel de la Guarda, Salsipuedes, and San Lorenzo Norte, on the basis of one shed skin from each. The first (SDSNH 19989) was collected in Arroyo Estatón, on the west side of Isla Angel de la Guarda, by Chris Parrish, June 6, 1961. This shed skin is nearly complete, with only a few of the head scales and the tip of the tail missing. It has 248 ventrals, 61+ subcaudals, and 23 scale rows at midbody. The skin is 1480 mm. long.

The second shed skin (SDSNH 45150) was found by Soulé on Isla San Lorenzo Norte, March 24, 1962, and the third (SDSNH 45003) by Richard C. Banks on Isla Salsipuedes

October 23, 1964. Both are incomplete, and the identifications are questionable. However, the characters of smooth scales in 23 rows, paired scale pits, undivided anal, divided subcaudals, and an alternating dark and light pattern eliminated other kinds of snakes considered possible by us. No snakes have previously been reported from these two islands.

Two living specimens have recently been collected on Isla Monserrate. An immature male (SDSNH 44631) was found in sand dunes on the northeast side of the island by Sloan on the evening of April 28, 1964. The total length is 482 mm., and the tail length is 67 mm. It has 235 ventrals, 54 subcaudals, 25 scale rows at midbody, 7-7 supralabials, and 10-11 infralabials. There are 38 light rings on the body and eight on the tail. An immature female (SDSNH 44632) was collected at the north end of the island by Richard C. Banks on June 24, 1964. This snake has a total length of 452 mm., and tail length of 56 mm. It has 243 ventrals, 49 subcaudals, 25 scale rows at midbody, 7-7 supralabials, and 11-10 infralabials. There are 37 light rings on the body and eight on the tail. Both snakes have light rings 1-2 scales long which are separated by 4-6 dark scales. These specimens are very similar to those found on the desert slopes of San Diego County, California.

Phyllorhynchus decurtatus decurtatus (Cope). An immature male (SDSNH 44682) was collected in Arroyo de Aquada, on the northeast side of Isla San José, by George E. Lindsay on June 26, 1964. The total length of this snake is 230 mm., and the tail length is 30 mm. There are 153 ventrals, 33 subcaudals, and 19 scale rows at midbody. There are 23 dark blotches on the body and five on the tail. The blotches near the head are rectangular, those near the anus are square. Most of them are rounded diamonds, 3-4 scales (end to end) long, occupy 6-7 scale rows, and are separated by three scales (end to end).

Except for the low number of ventrals and the shape of the blotches, this specimen agrees with the description of *P. d. decurtatus* (as redefined by Klauber, 1940b:206), but it keys out to *P. d. norrisi* (Savage and Cliff, 1954:74). This snake is abnormal in having the first infralabial on the right side split transversely, and the frontal incompletely separated from the single scale occupying the prefrontal area. This is the first insular record for this subspecies.

Phyllorhynchus decurtatus perkinsi Klauber. An immature female (SDSNH 52000) was collected on a sand dune at the northeast end of Isla Angel de la Guarda by Sloan, March 20, 1963. It was found about one hour after sundown among the exposed roots of *Atriplex polycarpa*. This is the first island record for this subspecies.

The total length of this snake is 263 mm., the tail length, 24 mm. It has 183 ventrals, 29 subcaudals, and 19 scale rows at midbody. There are 43 dark blotches on the body and four on the tail. The blotches near midbody are two scales (end to end) long and are separated by 2-3 scales (end to end). The length of the interspaces is less than in typical specimens of this subspecies (Klauber, 1935), and in this respect this snake is similar to a specimen of *P. d. decurtatus* from central Baja California reported by Murray (1955:45). The high ventral and blotch counts, however, indicate a close relationship to populations in northeastern Baja California and southeastern California rather than to those in southern Baja California.

Pituophis melanoleucus affinis Hallowell. An adult female (SDSNH 44387) was collected by Soulé at Bahía Agua Dulce, on the north end of Isla Tiburon, March 18, 1962. This snake is 1555 mm. long, including the 175 mm. tail. There are 240 ventrals, 61 subcaudals, and 33 scale rows at midbody. There are 46 dark body blotches, and 11 tail blotches. The supralabials are 9-9 (the fifth enters the orbit on each side), and the infralabials are 14-14; there are two pre- and four postoculars on each side.

In meristic characters, and in general appearance, this specimen is readily assigned to the subspecies *affinis*, which occurs on the adjacent mainland of Sonora, Mexico. Some peculiarities, however, seem worthy of note. The anterior nasal on each side is divided transversely, and there are creases on several head scales including the frontal, rostral, some infralabials and genials. A single shortened, irregularly shaped scale occupies the parietal region. There are three loreals on each side; the lower one is very small and does not contact the nasal or preocular. There are two series of scales in the prefrontal area, an anterior row of four followed posteriorly by a row of three.

This appears to be the first definite Gulf record of a gopher snake; it is surprising that such a large diurnal snake could have escaped detection for so many years, but perhaps it is a recent immigrant.

Rhinocheilus lecontei lecontei Baird and Girard. An adult male was collected by Richard C. Banks and Soulé near the former Ruffo Ranch, on the southwest side of Isla Cerralvo, October 29, 1961. Due to misidentification, this specimen was reported as *Lampropeltis getulus conjuncta* (Banks and Farmer, 1963). The genus *Rhinocheilus* has not previously been reported from any Gulf island. Cerralvo is approximately 540 miles southwest of Cape Colnett, the southernmost record for the genus in Baja California considered reliable by Klauber (1941:300).

The total length of this snake is 1100 mm., including the 146 mm. tail. There are 210 ventrals, 53 subcaudals (the first 35 are entire), and 23 scale rows at midbody. There are 25 dark blotches on the body, and nine on the tail.

This specimen (Calif. Acad. Sci. 98095) is reported through the courtesy of A. E. Leviton.

Tantilla planiceps (Blainville). One of the more interesting discoveries made during the Belvedere expedition was the presence of a black-headed snake on Isla Carmen. The single female (SDSNH 44388) was collected near Bahía Marquer by Charles E. Shaw and George E. Lindsay, April 4, 1962. It is 284 mm. long including the 66 mm. tail. There are 179 ventrals, 65 subcaudals, and 15 scale rows at midbody. In preservative, the specimen is uniform brown posterior to the head, all scale rows being pigmented. The black head cap extends down approximately to the angle of the mouth. The light nuchal band is one scale wide, and is bordered behind by four small dark brown spots.

Crotalus atrox Baird and Girard. The discovery of two specimens on Isla Santa Cruz is a new insular record for this species. They were collected on the west side of this island by Reid Moran and Chris Parrish on April 18, 1962.

An adult male (SDSNH 44350) has a total length of 909 mm., a tail length of 70 mm., and a head length of 41 mm. It has 183 ventrals, 22 subcaudals, 25 scale rows at midbody, 16-15 supralabials, 16-16 infralabials, 39 body blotches, and four tail blotches. An adult female (SDSNH 44351) has a total length of 737 mm., a tail length of 48 mm., and a head length of 34 mm. It has 181 ventrals, 17 subcaudals, 25 scale rows at midbody, 15-15 supralabials, 18-18 infralabials, 31 body blotches and four tail blotches. Both have 12 scales bordering the proximal rattle segment, and 15 scale rows at the middle of the tail.

The male was heavily infested with the parasitic linguatulid *Porocephalus crotali*. These were present nearly the entire length of the respiratory tract, with one actually occluding the glottis. The majority, including females heavily laden with eggs, were found in the anterior portion of the lung, which was distended and nearly filled the body cavity. Only a few parasites were found in the posterior portion of the lung; these included an attached individual opposite ventral 104.

Cliff (1954b:80) reported the first specimen of *Crotalus atrox* from Isla San Pedro Mártir. Members of the Belvedere expedition collected six additional specimens on the east side of this island on March 21, 1962. Measurements and scale counts are summarized in table 2. Cliff mentioned the possibility of this being a dwarf population on the basis of the single individual. It is true that these additional specimens also have relatively shorter heads than mainland specimens, but in the absence of other differences the recognition of an insular subspecies is not warranted.

Crotalus catalinensis Cliff. Two specimens of this recently described species (Cliff, 1954b:80) were collected on Isla Santa Catalina by members of the Belvedere expedition. During 1964, 10 additional specimens were secured by various individuals. Data now being accumulated on this interesting rattlesnake will be published separately.

Crotalus enyo enyo (Cope). An immature male (SDSNH 44355) was collected at Los Ostiones, on the northwest side of Isla San José by Richard C. Banks and William K. Emerson, April 12, 1962. This subspecies had been known previously from Islas San Francisco, Carmen, and Espíritu Santo (including Partida portion) in the Gulf of California (Klauber, 1956:122).

TABLE 2

Measurements (in mm.) and scale counts for *Crotalus atrox* from Isla San Pedro Mártir

SDSNH Catalog Number	44344	44345	44346	44347	44348	44349
Sex	Male	Male	Male	Female	Male	Male
Total length	1410	911	1369	940	1390	1293
Tail length	104	73	101	59	107	108
Head length	48	35	48	36.5	51.5	45
Ventrals	182	182	183	185	182	185
Subcaudals	28	27	28	22	28	28
Scale rows	25	25	25	26	25	25
Supralabials	15-15	15-15	15-15	15-14	16-16	15-15
Infralabials	16-17	18-17	17-17	17-17	17-17	17-17
Scales bordering rattle	11	11	12	11	10	10
Scale rows at mid-tail	13	15	15	13	14	15

The total length of this snake is 659 mm.; the tail length is 69 mm. There are 174 ventrals, 27 subcaudals, 25 scale rows at midbody, and 13 scale rows at the middle of the tail. There are 13-13 supralabials, and 14-14 infralabials. The proximal rattle segment is black, and is bordered by 10 scales. There are 36 body blotches and six tail blotches.

This specimen seems to fall within the range of variation of the subspecies *enyo* as defined by Klauber (1931b:363) in meristic characters and coloration, but it lacks preciliary scales and the lower loreal is slightly larger than the upper on both sides. The presence of this species was expected on Isla San José since it has been known to occur on nearby Isla San Francisco for many years.

Crotalus mitchelli mitchelli (Cope). An adult male (SDSNH 45002) was collected at the north end of Isla Monserate by Richard C. Banks, June 24, 1964. The total length of this snake is 810 mm., and the tail is 60 mm.; the head is 29 mm. long (contained in the total length 27.9 times). There are 173 ventrals, 24 subcaudals, and 23 scale rows at midbody. There are 14-14 supralabials (the last conspicuously larger than the one preceding), and 15-15 infralabials. The body has 37 blotches, and the tail, five. Speckled rattlesnakes have not previously been reported from this island.

Klauber (1956:38, 122) listed *C. m. mitchelli* on Isla Santa Cruz. This appears to be an error, and Klauber (personal communication) advises us to delete this island from the range.

THE ENVIRONMENT

Climatic and Vegetational Patterns.—The Gulf of California is a roughly rectangular body of water about 1400 km. long and from about 100 km. to 200 km. wide. It lies between the peninsula of Baja California to the west and the mainland Mexican states of Sonora and Sinaloa to the east. Although geographically the Gulf is in the Temperate Zone, its marine biota is predominantly Panamic (eastern tropical Pacific), reflecting the isolation of the Gulf from the cool water and air masses of the northern Pacific. The marine inlet to the Gulf is at 23° North Latitude, 50 km. south of the Tropic of Cancer.

The almost complete encirclement by land imposes on the Gulf and its islands a climate like that of an inland body of water, marked by extreme seasonal variation in air and water temperatures. This is especially true at the northern end of the Gulf, as illustrated by the annual variation of the surface temperatures of its waters. At Puerto Peñasco in the north, the annual range is 16° C (14.9° C in January to 31.2° C in August); at Cabo San Lucas in the south, on the Pacific side, the annual range is about 9° C (19.8° C in January to 29.1° C in August) (Roden and Groves, 1959). Similarly, air temperature extremes are greater in the northern Gulf coast area than in the southern (Roden, 1958).

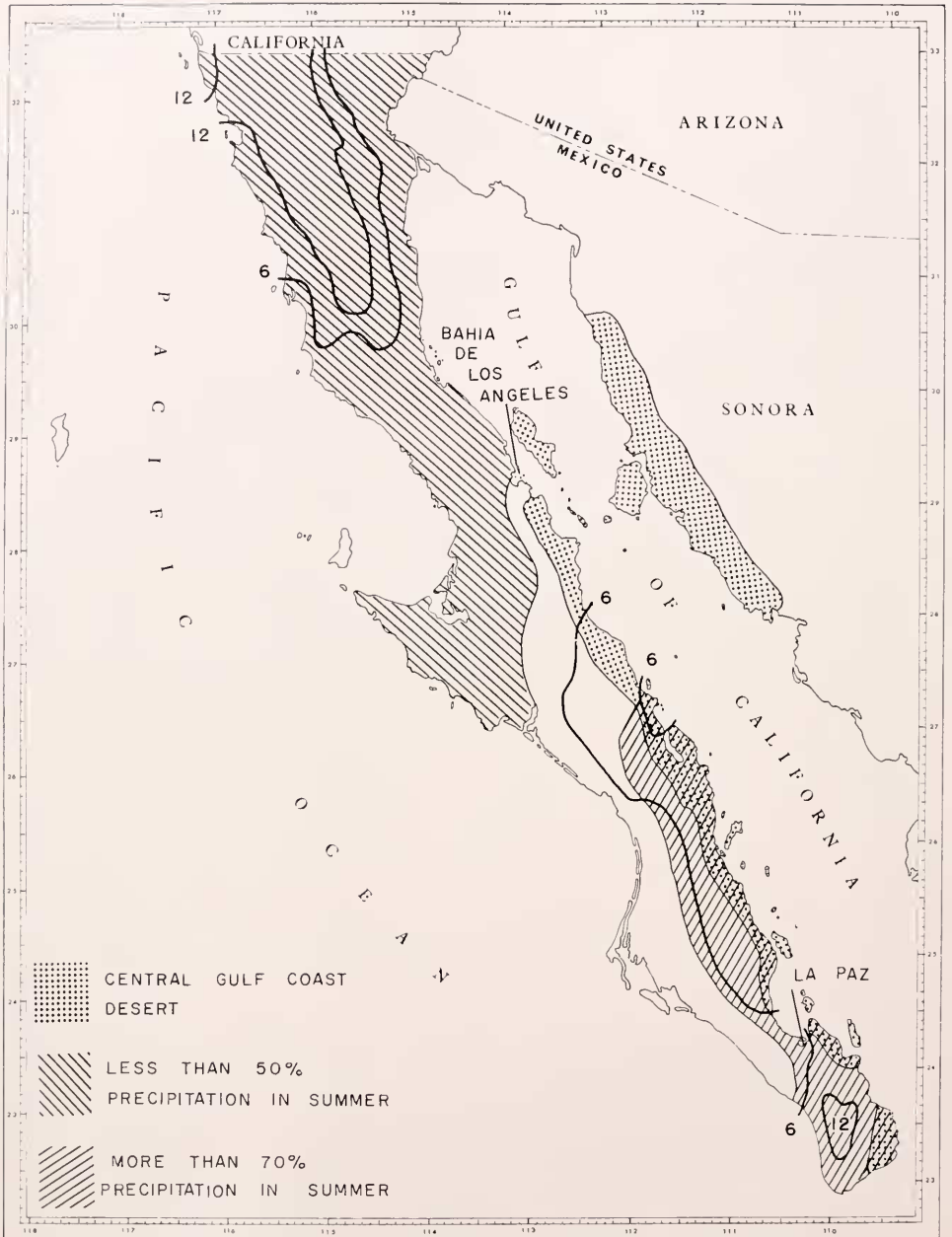


Fig. 2. Baja California and the Gulf of California. Precipitation belts are indicated by isoprecipitation lines. Numbers refer to inches of rainfall per year. (Adapted from Aschmann, 1959, and Shreve and Wiggins, 1964.)

The Gulf islands and the surrounding continental areas are extremely arid. Except for part of the Cape Region and the southernmost 400 km. of the mainland coast, the Gulf coast and adjacent areas lie entirely within the boundaries of the Sonoran Region of the North American Desert (Shreve and Wiggins, 1964). All but the southernmost parts of the Gulf probably receive less than seven inches of rain annually (fig. 2), although occasional hurricanes, known locally as "chubascos", may bring more than this amount within a few hours. At such times the typically dry arroyos become torrents.

The data pertaining to the rainfall pattern over the peninsula have been summarized by Aschmann (1959). He found that in the northern peninsular area to Bahía de los Angeles (29° N. Lat.), most of the precipitation is from Pacific cyclonic storms, and occurs in the winter. The actual amount of precipitation from these storms is slight, however, because this part of the Gulf coast is in the rain shadow of the lofty Sierra San Pedro Mártir and Sierra Juárez. Aschmann pointed out that most of the precipitation from the vicinity of Santa Rosalía (27° 20' N. Lat.) southward is from convective showers and chubascos and occurs in the summer (fig. 2). The central part of the peninsula lies between the northern winter storm belt and the southern summer storm belt. Few records are kept in this area, but it seems that some parts may receive less than three or four inches annually, and even this meager amount is not dependable. In fact, droughts lasting a year or longer have been reported.

With the exception of the Islas Las Encantadas group in the north, Shreve and Wiggins (1964) considered all of the Gulf islands studied here to be in the Central Gulf Coast subdivision of the Sonoran Desert (fig. 2). In emphasizing the vegetational uniformity of this region, Shreve states: "Throughout the two parts of this area [the central regions of both Gulf coasts] the vegetation is almost identical in physiognomy, and a large number of its component species are the same" (Shreve and Wiggins, 1964: 53). As in desert areas in general, vegetation is tallest and thickest in arroyos and at the bottoms of canyons. It is generally true that the larger the water course, the lusher the vegetation along its banks. Hillsides on some of the northern islands are completely barren of seed plants.

Shreve designated this desert the *Bursera-jatropha* region because of the relative abundance of these thick-trunked, deciduous trees. Other common genera of shrubs and trees of the area are *Olneya*, *Cercidium*, *Fouquieria*, *Prosopis*, *Larrea*, *Viscainoa*, *Maytenus*, *Stegnosperma*, *Encelia*, *Lycium*, *Euphorbia*, *Atriplex*, *Franseria*, and *Fagonia*. In some areas cacti are very abundant and may be the dominant plants locally. The most common of the larger forms of cacti are *Pachycereus pringlei*, *Machaerocereus gummosus*, *Lophocereus schottii*; *Lemaireocereus thurberi*, cylindrical forms of *Opuntia*, and species of *Ferocactus*.

Granting the overall vegetational uniformity of the Central Gulf Coast and the adjacent islands, there are, nevertheless, two vegetational gradients associated with the seasonal differences in the amount and pattern of precipitation. First, the amount of rainfall increases from the central Gulf area to the southern Gulf area. This produces a denser and taller vegetational aspect, especially in the large arroyos, southward from about Isla San Marcos to Isla Cerralvo. A possible faunistic concomitant of this north-south precipitation gradient is the restriction of amphibians to the southernmost islands, Islas Espíritu Santo-Partida Sur and Cerralvo (table 1). Second, the farther south one goes in the Gulf, the more the precipitation tends to be restricted to the summer months. The result is a higher proportion of plants in the south whose germination and flowering depend on this periodicity of the tropical weather pattern.

Geological History.—Biogeographic analysis is facilitated if the area under study has had a relatively quiet and unspectacular geological history. Such is not the case with the Gulf and the adjacent peninsular region. Recent geological and oceanographic research has shown that the shoreline of the Gulf basin has long been a dynamic physiographic feature. Apparently there has been extensive tectonic activity in the region, at least since the mid-Cretaceous orogeny (Durham and Allison, 1960). For the present purpose, however, it is unnecessary to trace the geological developments occurring before the late Cenozoic since the biogeographic and evolutionary patterns found in the islands today are probably interpretable, in large part, as the result of Pleistocene events.

The most far-reaching Pleistocene events were the cyclic glaciations. Changes in the eustatic sea level associated with the advance and retreat of Pleistocene continental ice sheets must have repeatedly modified the shoreline of the Gulf, alternately creating and drowning islands. It is generally agreed by geologists that the water trapped in ice sheets during the last glaciation accounted for a drop in sea level of approximately 110 meters. These ice sheets began to recede about 17,000 years ago, the sea level having risen to its present level about 6,000 years ago (Fairbridge, 1960; Godwin, Suggete and Willis, 1958). This last eustatic rise inundated large parts of the coast and created many of the offshore islands in the Gulf. Eustatic fluctuations have probably not amounted to more than a foot or so for the last 4,000 years (Russell, 1963). If crustal movements are ignored, it is reasonable to assume that those islands separated from the mainland by less than 110 meters depth (fig. 1) are less than 17,000 years old.

This category of probable recent or young shallow-water islands includes Islas Tiburon, San Marcos, Coronados, San José, San Francisco, and Espíritu Santo, as well as many small coastal and satellite islands.

The apparent tectonic instability of the region around the islands of Carmen, Monserrate and Danzante precludes accurate dating of these islands at this time. This instability is strikingly shown by Pleistocene wave-cut terraces at elevations of 250 to 300 feet in the vicinity of Santa Rosalía and on Islas Carmen and Monserrate (Anderson, 1950; Wilson and Rocha, 1955). Edward C. Wilson (personal communication) found evidence for a recent uplift amounting to about 250 feet on Salsipuedes. Tectonic activity is further evidenced by faulting and warping of Pleistocene sediments along the western margin of the Gulf (Anderson, 1950) accompanying the elevation of this area (Durham and Allison, 1960). All in all, eustatic changes can serve only as a very rough approximation of island age.

Some recent oceanographic investigations suggest that the great amount of volcanism, tectonic mobility, and overall geological diversity of the Gulf area are probably related to its geographical coincidence with the crest of the East Pacific Rise. The crest disappears at the southern end of the Gulf, but the exceptionally high flow of heat through the crust, as well as the frequency of shallow earthquakes in the Gulf area, both characteristic of the crest, attest to its extension into the Gulf (Menard, 1960). In fact, Menard's description (1960:1745) of the topography near the crest could easily be a description of the submarine topography of the Gulf: ". . . it appears to consist of volcanoes, low domes, and troughs with adjacent tilted fault blocks trending at various angles to the crest of the rise." Shepard (1950) concluded that the coastal and submarine scarps, as well as the extensive system of basins in the Gulf, are the result of faulting, some of it rather recently.

ENDEMICITY AND ITS BIOGEOGRAPHICAL CORRELATES

Johnston (1924) found that less than one per cent of the plants on the islands in the Gulf were endemic, and Gentry (1949) remarked, "The most striking aspect of the island floras is the apparent lack of divergent evolution." The terrestrial vertebrates, however, present quite a different picture. Nearly all of the mammals have been considered taxonomically distinct from their closest mainland relatives. In general, the reptiles also show a high degree of differentiation, although the percentage of endemics (about 20 per cent) is much lower than that for mammals.

Any comparison of endemicity between plants and animals must be subjective. Nevertheless, the striking difference in the frequency of endemics seems worthy of comment. Two reasons are suggested for this difference. First, dispersal in plants is generally more efficient over short stretches of water; accordingly, the relatively high rates of gene flow from mainland populations of plants to island populations would impede differentiation. Peter H. Raven suggested the second reason in conversation. Edaphic and climatic factors are probably paramount in the evolution of most plant species; since the islands and adjacent mainland coasts are apparently very similar in soil type and climate, little evolutionary adjustment would be expected.

It is probable that the difference in evolutionary divergence between the mammals and the reptiles, as indicated by taxonomic designation, is explicable partly as a difference in the characters used by the taxonomists dealing with the respective groups. Mammalogists rely heavily upon coat color differences in making taxonomic decisions about races; in rodents, especially, coat color is usually correlated with the substrate color (Dice and Blossom, 1937). Substrate-matching is common in reptiles as well, but herpetologists often ignore color because of the metachromatic capacities of many reptiles, and because reptile colors fade or are altered by preservation.

Populations of reptiles often seem to react to insular environments in predictable ways. Among the most frequently observed of these evolutionary tendencies is gigantism and "melanism" in lizards, and dwarfism in snakes (Klauber, 1963; Mertens, 1934). Insular gigantism, here meaning a larger mean body size than typically found in mainland populations, occurs in a number of forms on the deep-water, distant islands. Two species of chuckwallas, *Sauromalus varius* on Isla San Esteban and *S. hispidus* on most of the islands in the Isla Angel de la Guarda-San Lorenzo chain are bigger than the mainland forms. The Cerralvo Island whiptail lizard, *Cnemidophorus ceralbensis*, seems to be a gigantic insular derivative of the orange-throated whiptail lizard, *C. hyperythrus*. One of us (Soulé, 1966) studied gigantism in the side-blotched lizards (*Uta stansburiana*, *sensu lato*) of the Gulf islands. The largest utas occur on Isla San Pedro Mártir and on the Islas San Lorenzos; *Uta* is the only sceloporine lizard on those islands. It was concluded that the presence of other sceloporine lizards somehow inhibits an evolutionary increase in body size, and that the level of inhibition is inversely proportional to the square root of the number of sympatric sceloporine species. The large speckled rattlesnake of Isla Angel de la Guarda, *Crotalus mitchelli angelensis*, is an exception to the typical tendency for dwarfism in insular rattlesnakes in the Gulf (Klauber, 1963).

Insular melanism, or more generally, a dark albedo relative to the color of continental forms, is characteristic of some of the same populations mentioned in the discussion of gigantism. The utas on Islas San Pedro Mártir, San Pedro Nolasco, San Lorenzos, and Salsipuedes are noticeably darker than those on shallow-water islands or on the mainland. Similarly, the whiptail lizards on Islas San Lorenzos, San Pedro Mártir, and San Pedro Nolasco are relatively dark. The chuckwalla, *Sauromalus hispidus*, that is endemic to the Salsipuedes archipelago¹, is uniformly dark brown or black when adult. The significance of insular "melanism" is not definitely known, although the high rate of heat transference provided by a dark albedo would seem to be advantageous to ectotherms (see Kramer, 1949; Mertens, 1952).

SPECIES-AREA RELATIONSHIP

Population biologists have recently paid increasing attention to the challenging question of species diversity. Quantitative models capable of predicting the number and the relative abundance of species in a given area (with varying degrees of success) have been proposed by a number of authors (MacArthur, 1957; MacArthur and Wilson, 1963; Preston, 1962; Hairston, 1959; Hamilton *et al.*, 1963). Some of these models are more or less a matter of curve-fitting, while others rest on a combination of curve-fitting and theoretical considerations. It is the purpose of this section to describe the species-area phenomenon as it pertains to the vertebrate fauna of the Gulf islands. This analysis must be considered preliminary since it is only semi-quantitative and since new records of snakes are still being reported rather frequently.

The positive relationship between the numbers of species and the areas of islands is shown for terrestrial vertebrates (excluding birds and bats) in figure 3. A notable feature of this figure is the relative paucity of species on the deepwater, distant (from the mainland) islands.

¹The occurrence of this and other deep-water island forms of chuckwallas on shallow-water islands adjacent to the peninsula, e.g., on Islas Smith, Año Nuevo, Cabeza de Caballo, and Coronados, is very likely a reflection of the gustatory significance of these animals to the Indians that once occupied the region (see Aschmann, 1959).

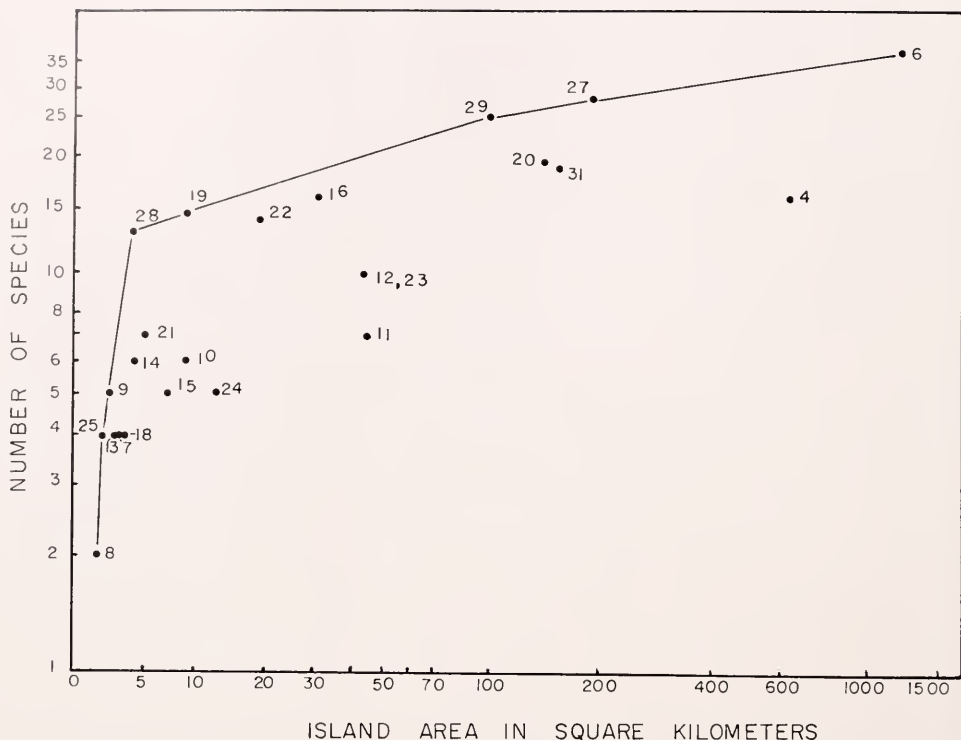


Fig. 3. Species-area relationship of terrestrial vertebrates (excluding bats and birds) on the major islands in the Gulf of California.

The line drawn through the upper points is a conservative "saturation curve" (see text). See fig. 2 for island-number key.

The curve drawn in this figure between the highest points (the greatest species abundance for their area) is a conservative estimate of the relationship between maximum species abundance and island area for terrestrial vertebrates in the Gulf.

MacArthur and Wilson (1963) have treated such data in an original way to demonstrate the "distance effect." Their method is applied to our data in figure 4; the abscissa represents the distance from the land mass that is the likeliest source of immigrants. The ordinate represents the percentage "saturation"; that is, the ratio of the number of species known on an island to an estimate of the maximum number of species possible (the curve in fig. 3). The obvious negative association is consistent with the findings of MacArthur and Wilson (1963) that the "equilibrium" number of species on an island is a function of its distance from the source of immigrants.

Recently, Preston (1962) has emphasized a most important point in distinguishing between the biotas of islands and of mainland areas. The biota of any mainland area is essentially a sample of the biota of a much larger region. Many of the species are represented by only a few individuals or by migrants and would not be expected to survive long if they were not periodically replenished from outside. On islands, replenishment is obviously less frequent than it is on most continental regions of equal size. As such, islands more closely approach the "correct" number of species for their areas. The view of MacArthur and Wilson is in general agreement with that of Preston, but emphasizes (1) the dynamic nature of the equilibrium—the actual equilibrium number for any island would be a biogeographical constant, but the species composition is constantly changing—and (2) the effect of distance from the source(s)

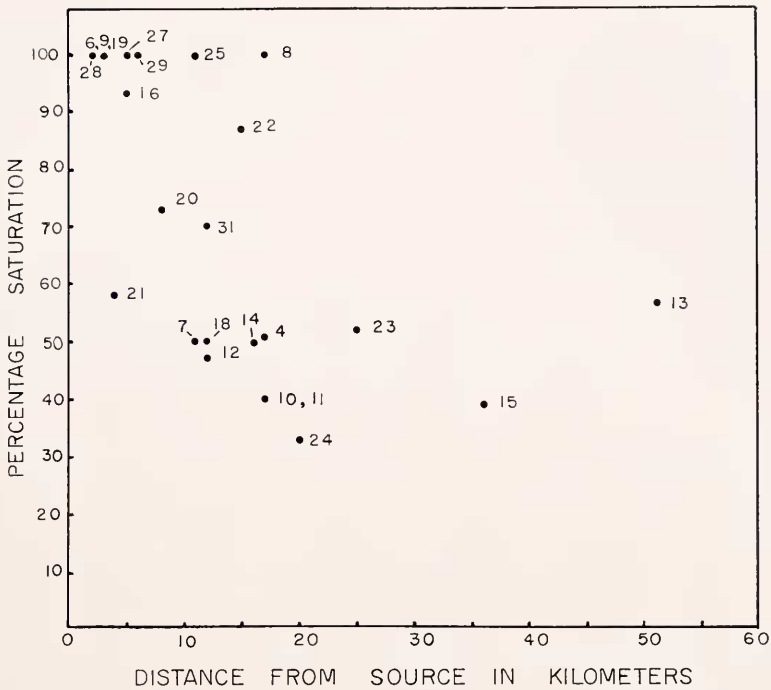


Fig. 4. Percentage saturation of terrestrial vertebrate faunas (excluding bats and birds) on major islands in the Gulf of California.

For *Islas Partida Norte*, *San Esteban*, *San Diego*, and *San Francisco*, the distance from the source is estimated from the nearest large island. For all other islands, the distance is measured from the mainland. See fig. 2 for island-number key.

of immigrants on the equilibrium number. Hamilton and Rubinoff (1963) demonstrate a distance effect relative to endemism of Darwin's Finches on the Galápagos Islands.

Most quantitative studies of insular biogeography have concerned oceanic islands. During the colonization of such islands the equilibrium number of species is approached from below by the gradual accumulation of successful colonizers. In contrast, continental islands are formed with their biotas intact. At the time of isolation the biota of a continental island is a sample of the mainland biota and includes more species than would be predicted for a biotically equilibrated island of comparable size and distance from the source(s) of immigrants. For continental islands, the approach to the equilibrium number of species would be from above, *i.e.*, extinction will proceed at a greater rate than will colonization. Consequently, the biotas of recently isolated continental islands are "supersaturated." It is problematical how long a biota will remain supersaturated. This depends on the organisms being considered, the nature and constancy of the physical environment, the size and ecological diversity of the island, and other factors.

With respect to the Gulf islands, the greater species abundance on the shallow-water islands could be attributed either to supersaturation or to the effect of distance on the equilibrium number. If further analysis confirms the fit of these data to the latter model, it would mean that equilibrium has been reached in the few thousands of years since these islands were formed.

The effects of species interactions on distribution and species abundance of reptiles on the Gulf islands is discussed elsewhere (Soulé, 1966).

SUMMARY

The distribution table lists some 250 records of insular occurrences of reptiles and amphibians of 33 genera (2 anurans, 14 lizards, 16 snakes, and 1 tortoise), from 31 islands in the Gulf of California. Of these genera, only the lizard genus *Sator* is endemic to the Gulf. Most of the 60 species, including the two amphibians and the tortoise, are considered mainland forms. Twelve of the species are sufficiently divergent from the mainland species to be considered endemic to the Gulf. Most of the endemic subspecies are isolated populations of widely distributed mainland species.

Extensions of the known range to additional islands in the Gulf of California or first reports of occurrence on any Gulf island are given for 12 species of snakes.

Insular gigantism and melanism are discussed, and examples from the Gulf herpetofauna are given. The relationship of the number of terrestrial vertebrates to the size of the island, and to the distance from the probable source of immigrants, is discussed and illustrated. A positive correlation is demonstrated for the former, and a negative correlation for the latter.

LITERATURE CITED

- ANDERSON, C. A.
1950. 1940 E. W. Scripps cruise to the Gulf of California. Part 1. Geology of islands and neighboring land areas. Geol. Soc. Amer. Mem. 43. 53 pp.
- ASCHMANN, H.
1959. The central desert of Baja California: Demography and ecology. Ibero-Americana: 42. Univ. Calif. Press, Berkeley. 282 pp.
- BANKS, R. C., AND W. M. FARMER
1963. Observations on reptiles of Cerralvo Island, Baja California, México. Herpetologica 18:246-250.
- BANTA, B. H., AND A. E. LEVITON
1963. Remarks on the colubrid genus *Chilomeniscus* (Serpentes: Colubridae). Proc. Calif. Acad. Sci., 4th Ser., 31:309-327.
- CLIFF, F. S.
1954a. Variation and evolution of the reptiles inhabiting the islands in the Gulf of California, Mexico. Unpublished Ph. D. dissertation. Stanford Univ.
1954b. Snakes of the islands in the Gulf of California, Mexico. Trans. San Diego Soc. Nat. Hist. 12:67-98.
1958. A new species of *Sauromalus* from Mexico. Copeia 1958:259-261.
- CRIPPEN, R. G.
1962. Two new insular records of amphibians from Baja California. Herpetologica 18:137.
- DICE, L. R., AND P. M. BLOSSOM
1937. Studies of mammalian ecology in southwestern North America with special attention to the colors of desert mammals. Carnegie Inst. Wash. Publ. 485. 129 pp.
- DICKERSON, M. C.
1919. Diagnoses of twenty-three new species and a new genus of lizards from Lower California. Bull. Amer. Mus. Nat. Hist. 41:461-477.
- DIXON, J. R.
1964. The systematics and distribution of lizards of the genus *Phyllodactylus* in North and Central America. New Mexico State Univ. Research Center, Sci. Bull. 64:1. 139 pp.
- DURHAM, J. W., AND E. C. ALLISON
1960. The geologic history of Baja California and its marine faunas. Syst. Zool. 9:47-91.
- ETHERIDGE, R.
1961. Additions to the herpetological fauna of Isla Cerralvo in the Gulf of California, Mexico. Herpetologica 17:57-60.

- FAIRBRIDGE, R. W.
1960. The changing level of the sea. *Sci. Amer.* 202 (5) : 70-79.
- FIGG-HOBLYN, J. P., AND B. H. BANTA
1957. *Lampropeltis getulus conjuncta* (Cope) on Cerralvo Island, Gulf of California, Mexico. *Herpetologica* 13:192.
- GENTRY, H. S.
1949. Land plants collected by the *Velero III*, Allan Hancock Pacific Expedition 1937-1941. *Allan Hancock Pac. Exped.* 13:5-245.
- GODWIN, H., R. P. SUGGATE, AND E. H. WILLIS
1958. Radiocarbon dating of the eustatic rise in ocean-level. *Nature* 181:1518-1519.
- HAIRSTON, N. G.
1959. Species abundance and community organization. *Ecology* 40:404-416.
- HAMILTON, T. H., AND I. RUBINOFF
1963. Isolation, endemism, and multiplication of species in the Darwin finches. *Evolution* 17:388-403.
- HAMILTON, T. H., I. RUBINOFF, R. H. BARTH, JR., AND G. L. BUSH
1963. Species abundance: natural regulation of insular variation. *Science* 142:1575-1577.
- JOHNSTON, I. M.
1924. Expedition of the California Academy of Sciences to the Gulf of California in 1921. The botany (The vascular plants). *Proc. Calif. Acad. Sci.*, 4th ser., 12:951-1218.
- KLAUBER, L. M.
1931a. A new subspecies of the California boa, with notes on the genus *Lichanura*. *Trans. San Diego Soc. Nat. Hist.* 6:305-318.
1931b. *Crotalus tigris* and *Crotalus enyo*, two little known rattlesnakes of the Southwest. *Trans. San Diego Soc. Nat. Hist.* 6:353-370.
1935. *Phyllorhynchus*, the leaf-nosed snake. *Bull. Zool. Soc. San Diego* No. 12. 31 pp.
1940a. The worm snakes of the genus *Leptotyphlops* in the United States and northern Mexico. *Trans. San Diego Soc. Nat. Hist.* 9:87-162.
1940b. Two new subspecies of *Phyllorhynchus*, the leaf-nosed snake, with notes on the genus. *Trans. San Diego Soc. Nat. Hist.* 9:195-214.
1941. The long-nosed snakes of the genus *Rhinocheilus*. *Trans. San Diego Soc. Nat. Hist.* 9:289-332.
1956. *Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind*. Univ. Calif. Press, Berkeley. 2 vol. xxix + 1476 pp.
1963. A new insular subspecies of the speckled rattlesnake. *Trans. San Diego Soc. Nat. Hist.* 13:73-80.
- KRAMER, G.
1949. Über Inselmelanismus bei Eidechsen. *Z. Ind. Abst. u. Vererb.* 83:157-164.
- LINDSAY, G. E.
1962. The Belvedere expedition to the Gulf of California. *Trans. San Diego Soc. Nat. Hist.* 13:1-44.
- LOWE, C. H., JR., AND K. S. NORRIS
1955. Analysis of the herpetofauna of Baja California, Mexico. III. New and revived reptilian subspecies of Isla de San Esteban, Gulf of California, Sonora, Mexico, with notes on other satellite islands of Isla Tiburon. *Herpetologica* 11:89-96.
- MACARTHUR, R. H.
1957. On the relative abundance of bird species. *Proc. Nat. Acad. Sci.* 43:293-295.
- MACARTHUR, R. H., AND E. O. WILSON
1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373-387.
- MAYR, E.
1942. *Systematics and the Origin of Species*. Columbia Univ. Press, New York. 334 pp.

- MENARD, H. W.
1960. The East Pacific Rise. *Science* 132:1737-1746.
- MERTENS, R.
1934. Die Insel-Reptilien, ihre Ausbreitung, Variation, und Artbildung. *Zoologica* 32:1-209.
1952. Schwarzblaue Insel-Eidechsen und die neueren Ansichten über ihr Farbkleid. *Natur u. Volk* 82:386-395.
- MURRAY, K. F.
1955. Herpetological collections from Baja California. *Herpetologica* 11:33-48.
- PRESTON, F. W.
1962. The canonical distribution of commonness and rarity. Parts I, II. *Ecology* 43:185-215, 410-432.
- RODEN, G. I.
1958. Oceanographic and meteorological aspects of the Gulf of California. *Pacific Sci.* 12:21-45.
- RODEN, G. I., AND G. W. GROVES
1959. Recent oceanographic investigations in the Gulf of California. *Jour. Mar. Res.* 18:10-35.
- RUSSELL, R. J.
1963. Recent recession of tropical cliffy coasts. *Science* 139:9-15.
- SAVAGE, J. M., AND F. S. CLIFF
1954. A new snake, *Phyllorhynchus arenicola*, from the Gulf of California, Mexico. *Proc. Biol. Soc. Wash.* 67:69-76.
- SCHMIDT, K. P.
1922. The amphibians and reptiles of Lower California and the neighboring islands. *Bull. Amer. Mus. Nat. Hist.* 46:607-707, pl. 47-62.
- SHAW, C. E.
1945. The chuckwalla, genus *Sauromalus*. *Trans. San Diego Soc. Nat. Hist.* 10:269-306.
- SHEPARD, F. P.
1950. 1940 E. W. Scripps cruise to the Gulf of California. Part III. Submarine topography of the Gulf of California. *Geol. Soc. Amer. Mem.* 43. 32 pp.
- SHREVE, F., AND I. L. WIGGINS
1964. *Vegetation and Flora of the Sonoran Desert.* Stanford University Press. 2 vol. x + 1740 pp.
- SMITH, H. M., AND E. H. TAYLOR
1945. An annotated checklist and key to the snakes of Mexico. *U. S. Nat. Mus. Bull.* 187. 239 pp.
1950. An annotated checklist and key to the reptiles of Mexico exclusive of the snakes. *U. S. Nat. Mus. Bull.* 199. 253 pp.
- SOULÉ, M. E.
1961. *Eridiphas slevini* (Tanner) on Cerralvo Island, Gulf of California, Mexico. *Herpetologica* 17:61.
1966. Trends in the insular radiation of a lizard. *Amer. Nat.* 100:47-64.
- VAN DENBURGH, JOHN
1922. The reptiles of western North America. *Occ. Pap. Calif. Acad. Sci.* no. 10. 2 vol. 1028 pp.
- WILSON, I. F., AND V. S. ROCHA
1955. Geology and mineral deposits of the Boleo copper district, Baja California, Mexico. *U. S. Geol. Survey Prof. Paper* 273. 134 pp.
- ZWEIFEL, R. G., AND K. S. NORRIS
1955. Contribution to the herpetology of Sonora, Mexico: Descriptions of new subspecies of snakes (*Micruroides euryxanthus* and *Lampropeltis getulus*) and miscellaneous collecting notes. *Amer. Midl. Nat.* 54:230-249.